

Evaluating cognitive penetrability of perception across the senses

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Abstract

A central question about the human mind is whether perception is an encapsulated process purely driven by sensory information or whether perception is intricately linked with cognitive processes. This debate about the cognitive penetrability of perception is discussed in psychology, cognitive neuroscience, and philosophy. So far, the debate has centered on vision, without major attempts to examine other senses. In this Review, we provide an overview of the key empirical evidence about cognitive penetrability of perception in vision, audition, somatosensation (including proprioception and pain perception), vestibular perception, and chemosensation (gustation, chemesthesis and olfaction). We conclude that many, but not all, of the senses are cognitively penetrable. Specifically, cognitive penetrability seems to vary with the extent to which a sense is intrinsically multimodal, receives indirect cognitive influences, and whether hedonic evaluation is an integral aspect of the perceptual experience. We suggest that the debate about cognitive penetrability needs to be more differentiated with respect to the sensory modality of the perceptual experience and the diversity of cognitive influences on that modality.

Introduction

Perception of the world by human senses might be influenced by one's thoughts, knowledge and memory contents. Alternatively, perception might operate independently of cognition. These two possibilities lie at the core of the debate about the 'cognitive penetrability' of perception, and have been intensely discussed in psychology, cognitive neuroscience, and philosophy of mind ¹⁻⁹. This debate relates directly to key questions in philosophy and brain sciences. For instance, if cognition influences perception, then perception would be a product of subjective experience and thought processes rather than a veridical representation of the outer world. Furthermore, cognitive penetration calls into question the distinction between cognition and perception and whether brain areas are exclusively dedicated to perception or cognition, or, alternatively, if intertwined processing across brain areas means an elimination of a clear distinction between cognition and perception.

The debate has recently gained momentum, fueled by philosophical proposals that argue that cognition and perception have distinct properties and formats ¹⁰, which raises the question of exactly how cognition and perception interact. The debate on cognitive penetrability of perception has to be resolved by considering empirical data, including evidence from neuroscience, which some previous discussions have neglected ². In addition, the debate about cognitive penetrability has so far almost exclusively focused on visual perception. Thus, specific characteristics of vision focus might have inadvertently shaped the debate.

Perception happens beyond just vision, so a comprehensive examination of cognitive penetrability should consider all senses to integrate evidence across subfields. Because different perceptual systems might be differentially susceptible to cognitive influences, here we push forward the debate on cognitive penetrability of perception by comparing different sensory modalities. If perception is truly impenetrable by cognition, it should be impenetrable across the senses. By contrast, if cognition does penetrate perception, the degree of penetrability might vary across the senses. Thus, fleshing out the differences and commonalities in cognitive penetrability between the senses based on empirical psychological and neuroscientific evidence has the potential to substantially advance and clarify the debate.

In this Review, we first briefly summarize the key arguments for and against cognitive penetrability of perception and provide an operational definition of cognitive penetrability. Then we present the key empirical evidence separately for vision, audition, somatosensation (including touch, proprioception and pain), vestibular perception, and chemosensation (including gustation, chemesthesis, and olfaction). We then step back to synthesize whether, for each sense, the evidence speaks for or against cognitive penetrability. Finally, we conclude and discuss future research directions.

Arguments for and against cognitive penetrability

Cognitive penetrability is usually defined as the influence of a higher cognitive state (such as memory contents, abstract knowledge, beliefs or intentions) on 'perceptual experience'. Perceptual experience is what philosophers of mind refer to as the phenomenal character of perception: 'what it is like' to experience a particular percept as the perceiver ⁴.

At the very core of the debate lies the intuitive idea that perception and cognition are separable processes in the mind, of different 'kinds' and with different qualities ¹⁰ (Fig. 1). Drawing a

theoretical distinction between perception and cognition does not per se argue for or against cognitive penetrability, but it lays the groundwork for presupposing different systems for cognition and perception and the question of how these two systems interact.

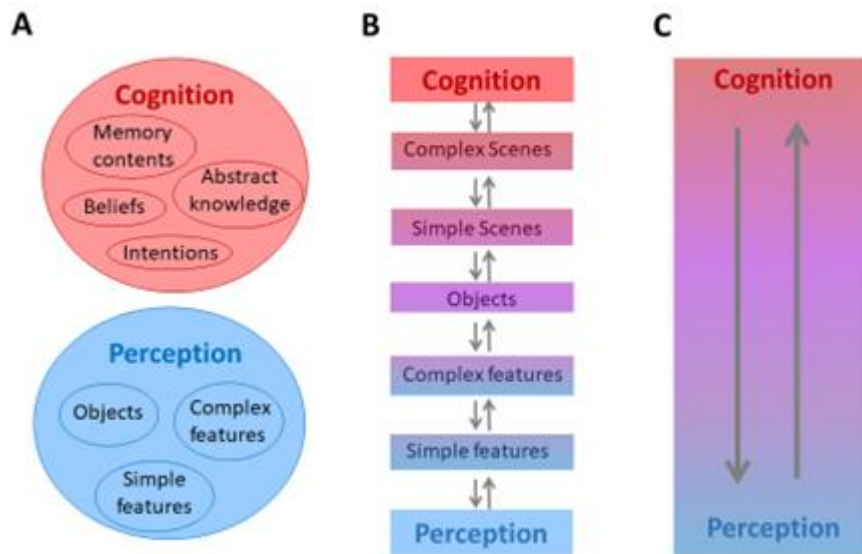


Figure 1. Possible relationships between cognition and perception. A) The impenetrability thesis. Perceptual processes, including low-level and high-level perceptual processes, happen in an ‘informationally encapsulated’ module that is separate from and impenetrable by cognitive processes ^{2,11,12}. B) One penetrability thesis. The theoretical distinction between high-level cognitive processes and low-level perceptual processes is maintained, but with a constant exchange between many intermediate processing stages in which cognition and perception are intermixed. Thus, cognitive penetration of perception is possible, even if not from every stage ^{5,9}. C) Another penetrability thesis. The border between cognition and perception is gradual and fuzzy, no clear boundary is defined and therefore penetration can happen in both directions ^{3,17}.

Early proponents of cognitive impenetrability usually presumed a strongly modular organization of the mind. Specifically, they argued that perceptual experience is the output of an ‘informationally encapsulated’ early sensory module that is separate from cognition ^{11,12}. In these earlier works, encapsulated modules are conceptualized as computational mechanisms that are specific to a cognitive domain, hardwired, computationally autonomous and restricted to a set of inputs without access to information stored in other modules¹¹. Because of this clear functional distinction between modules, the sensory module creates a perceptual experience without any direct influence of cognition. Yet, even early proponents¹² admitted that cognition could influence perception via indirect mechanisms, such as attention-driven enhancements of feature perception. Despite this admission, the view of an encapsulated and impenetrable perceptual module is still defended today ².

The idea of a strong modularity of the mind originated from evidence for the functional specialization of brain areas. For example, neuropsychology and early neuroimaging showed that perceiving colors activates brain area V4 and that lesions to V4 lead to a deficit in color perception ^{13,14}, whereas cognitive processes such as decision making activate frontal cortex

and lesions thereof lead to related cognitive deficits¹⁵. Accordingly, it was concluded that perception and cognition happen in separate and independently operating brain areas.

The time course of brain activity has also been used to argue for cognitive impenetrability. Neural data revealed that early sensory areas extract basic sensory features quickly after perceptual stimulation, and higher-level sensory areas processing more complex information later on¹⁶. These data led some theorists to claim that basic perceptual processes happen within the first 100 ms of processing, which is too rapid for any cognitive influences from higher brain areas such as frontal cortex⁷.

Another argument for cognitive impenetrability comes from the phenomenology of visual illusions. Famously, the Müller-Lyer illusion contains line segments of the same length that appear to have different lengths (Fig. 2A). Even if an observer is familiar with the illusion, the cognitive knowledge that the two lines are of equal length does not overcome the illusory percept. Thus, it is usually concluded that the illusory percept is impenetrable by cognitive knowledge.

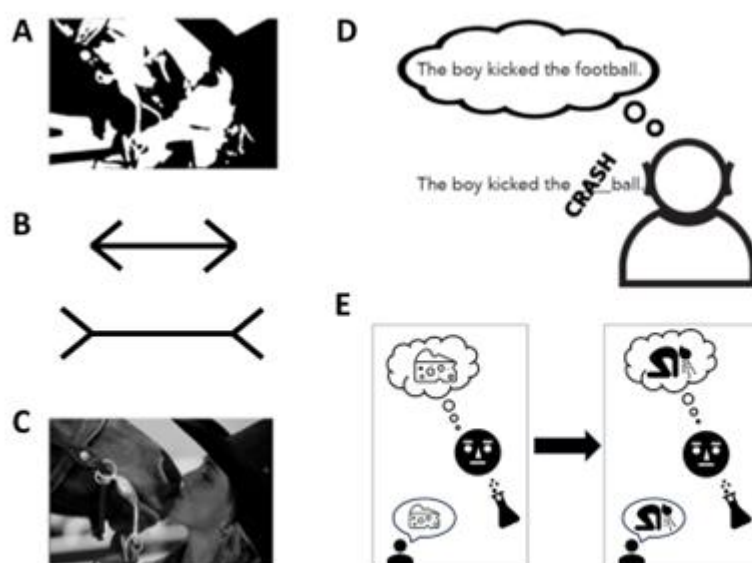


Figure 2. Top-down effects in different senses. Top-down effects in vision: **B)** This two-tone image seems like a meaningless assembly of black and white patches but becomes immediately recognizable once one has seen the full gray-scale photograph (**E**) ([shown here](#)) that provides contextual, high-level information. **B)** In the Müller-Lyer illusion, the two horizontal lines are of equal length but the upper line is usually perceived as shorter than the lower line due to the angled lines. Knowledge of the line length does not change the illusory perception of different lengths. **C)** In phonemic restoration, a listener perceives continuous speech from noise and fills in the missing content based on the surrounding context, often without being aware of a gap. Top-down effects in olfaction: **D)** Participants sample an odor that is labeled as either 'parmesan cheese' or 'vomit'. When the label differs, participants do not recognize the odor as being identical to the one they previously smelled²¹⁴. **E)** Full gray-scale photograph from which the image in **B)** was derived from.

Proponents of cognitive impenetrability also argue that the evidence for cognitive penetrability is insufficient and inconclusive, and therefore the presupposition of an impenetrable sensory module must be true ². For example, some have argued that psychological evidence for effects of cognition on perception reflect changes in the cognitive judgment of perceptual experience, not the experience itself ². Further, they argue that certain processes (including feature-based and object-based attention as well as object recognition) are part of the perceptual module and therefore influences of these processes on perception do not count as cognitive penetration. Here it becomes clear that one of the key sticking points in the cognitive penetrability debate is where to draw the boundary between perception and cognition. If the perceptual module is defined to encompass many high-level processes, then it is easier to argue against cognitive penetrability because cognitive processes within the module are defined as perceptual. By contrast, if the boundary for what counts as perception is set sufficiently low, then many top-down influences can count as cognitive penetration.

Proponents of cognitive penetrability often argue against a clear-cut boundary between perception and cognition. Some question the existence of a cognition-perception boundary altogether ^{3,17} (Fig. 1c). Others argue that even if one can maintain a distinction between predominantly cognitive processes (such as abstract mathematical reasoning) and predominantly perceptual processes (such as seeing a single light in darkness), the majority of functional everyday perception results from an interplay of different intermediate processing stages along the perceptual processing hierarchy, and is therefore a mixture of cognition and perception ^{5,9,18} (Fig. 1b).

Empirical evidence supports the view that almost all percepts are a product of both bottom-up sensory processes and top-down cognitive processes. For instance, modern neuroscience evidence shows that although there is functional specialization of brain areas, strict modularity of brain function, and particularly the idea of informational encapsulation, is inaccurate. On the anatomical level, the vast majority of cortical brain areas are heavily interconnected with each other through lateral, short-range, and long-range connections¹⁹. These connections make the existence of informationally encapsulated modules highly implausible. Instead, complex, recurrent dynamics of interacting bottom-up and top-down processes sculpt neural processing throughout the sensory hierarchies (Fig. 3). These dynamics are essential for functional perception, and influence all perceptual processes throughout the time course of processing, even shifting how neurons respond to the same sensory inputs to reflect top-down expectations and predictions ^{20–24}. Thus, attempts to draw a strict boundary between perception and cognition are motivated by theoretical arguments that seem to ignore modern knowledge about brain organization.

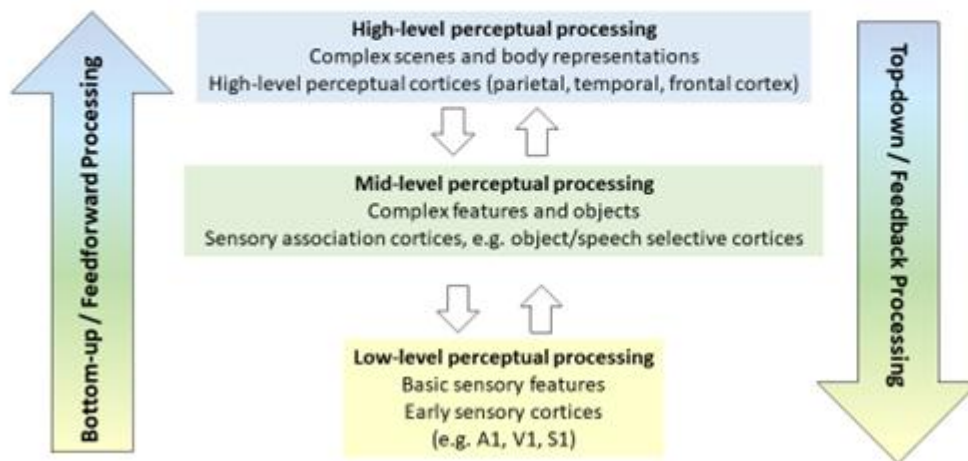


Figure 3. Hierarchical recurrent perceptual processing in the human brain.

Perceptual processing in vision, audition, olfaction, gustation and somatosensation occurs along a hierarchy through low-level, mid-level, and high-level processing. Brain areas responsible for the different processing stages are anatomically and functionally highly interconnected, and information constantly flows in both directions, bottom-up via feedforward connections and top-down via feedback connections to create conscious functional perception from complex and multisensory information. The vestibular system does not have a dedicated unimodal sensory cortex (as depicted here) but is instead supported by a widespread subcortical and cortical network.

However, the constant information exchange across different brain areas does not mean that each brain area arbitrarily interacts with every other brain area. Instead, information exchange is confined by structural and functional brain connectivity that plastically evolves during development and learning. The example of the Müller-Lyer illusion (Fig. 1a) nicely illustrates that not any cognitive knowledge (knowing that the two horizontal lines are of equal length) can influence any percept (that the bottom line looks longer). In fact, some theorists have argued that the Müller-Lyer illusion demonstrates a case for cognitive penetrability: growing up in man-made, mostly rectangular environments results in learned associations about the length of edges of floors and walls consistent with the upper line being longer. Thus, the Müller-Lyer illusion can be seen as a consequence of a cognitive inference about line length induced by the flanking arrowheads^{9,25}. This example demonstrates that different penetrating factors need to be distinguished; not every piece of cognitive knowledge can influence every perceptual experience. However, the reverse inference—that the lack of a specific cognitive influence implies that no cognitive state can penetrate perception—does not seem valid either, particularly when considering the evidence on recurrent information exchange and the evidence reviewed below.

Penetrating factors

There has been considerable debate on what counts as a cognitive factor and therefore what can be considered to penetrate perception. Feature-based and object-based visual attention have typically been included as penetrating factors as they depend primarily on task or

knowledge²⁶, which are considered cognitive. However, shifts of visual spatial attention have typically been excluded as penetrating factors⁴ because they can influence perceptual experience in a manner independent of cognitive content²⁷ and may change the state of the sensory organ similar to eye movements. Although discounting spatial attention as a cognitive factor seems intuitive in vision, it might make less sense in audition. Spatial and non-spatial auditory attention influence early auditory processing in a similar way, so the distinction between spatial attention and other forms of auditory attention is muddy and unclear. Changes in the external stimulus (such as brightness or loudness) that automatically draw exogenous attention are usually excluded as penetrating factors. Internally driven, endogenous attention is a more controversial case because endogenous attention can be purely spatial (as in the instruction to “attend left”), temporal (“attend now”), or cognitively driven (“look for the red bike” or “listen to the teacher’s voice”). Similarly, internally generated mental imagery can have more or less cognitive content²⁸. For the purpose of our Review, we focus on influences that carry cognitive content. Cognitive content includes, for example, semantic memory content, abstract or conceptual knowledge, or beliefs or intentions

There is a lot of evidence that temporal expectations, spatial expectations, and priors (the assumed probability of each of the different observable states of the environment) influence perception in touch, audition and vision, and potentially olfaction. However, the extent to which these factors count as cognitive states in the traditional definition of cognitive penetration is unclear. Priors reflect knowledge about the world but the information stored in priors is not always cognitively represented. For example, visual perception of tilted lines is influenced by a strong prior assumption that lines are typically either vertically or horizontally oriented²⁹ and prior assumptions about the location of the limbs are deeply embedded in the tactile system^{30,31}. Yet, even though these priors might mirror the statistics of the world, and thus are observable, most people whose perception is influenced by these priors would be unable to list them. Thus, most priors influence perception in the absence of explicit conscious awareness, whereas influences from cognitive content may, but do not have to be, accompanied by conscious awareness of that content.

The extent to which perceptual learning (long-term learning of statistical regularities arising in one’s sensory environment³²) counts as cognitive penetration of perception is also up for debate. For example, a bird watcher learning to recognize a species of bird goes through a learning process that involves explicit cognitive processing of the combination of features characterizing the bird, before the recognition process becomes automatic and therefore to some extent perceptual. Similarly, in olfaction, sweetness becomes an intrinsic perceptual property of odors such as vanilla after many instances of associative learning in which sweet and vanilla are experienced together. Some theorists argue that cognition penetrates perception at least during perceptual learning because cognitive knowledge about, for example, the features of a bird, affects later perceptual recognition of the bird⁸. However, other theorists have argued that perceptual learning can happen within the encapsulated perceptual module as being part of basic perceptual mechanisms, similar to feature-based attention or object recognition^{2,12}.

Whether emotional influences count as cognitive is also unclear. Although emotion and cognition are intricately intertwined, they are partly subserved by distinct brain pathways³³. Emotions have sometimes been conceptualized as perceptual³⁴) and in some sensory modalities the hedonic evaluation of a percept (such as the pleasantness of touch or spicy food) is an integral part of the perceptual experience. It is therefore difficult to classify emotions as clearly cognitive. Emotional penetration of perception has partly been reviewed elsewhere³⁵ and deserves its own discussion outside the scope of this review.

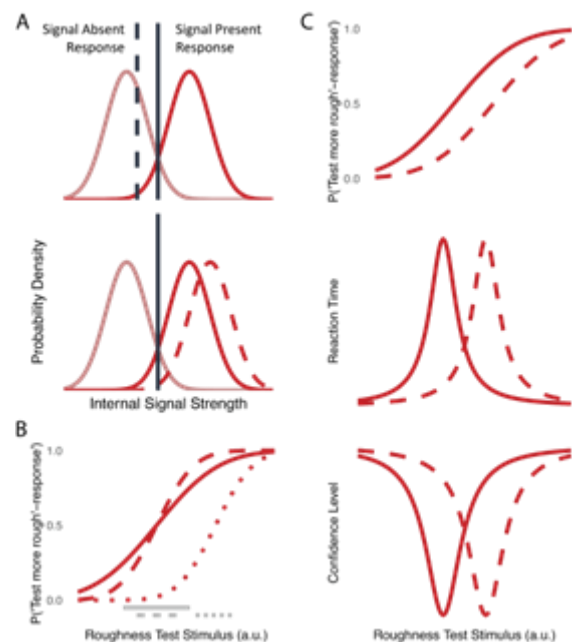
Overall, no firm conclusion can be drawn in either direction for any of these areas and each reinforce that the debate on cognitive penetrability critically hinges on what counts as cognitive.

Perceptual experience and evaluation

Another sticking point of the debate is what exactly is being penetrated or influenced by cognition. Philosophy of mind defines cognitive penetration as a cognitive influence on the phenomenology of perceptual experience. Proponents of cognitive impenetrability have often argued that it is not the perceptual experience itself that is being penetrated, but rather the judgment of this experience, which they argue is a cognitive, post-perceptual process. Accordingly, many psychological studies that show cognitive influences on perception have been discounted as involving such an influence^{1,2}. From an experimental point of view, it is not easy to disentangle perceptual experience from its judgment. In the laboratory, measuring perception usually requires participants to explicitly report aspects of their subjective percept (for example, the length of a line) which inevitably involves a conscious and cognitive judgment of the percept (for example, whether the line is longer or shorter than a reference line). These reports are susceptible to potentially cognitive response biases in decision making. Thus, biased responses in a behavioral experiment might not necessarily reflect perceptual biases. One way to circumvent this problem in behavioral experiments is to focus on perceptual sensitivity, which enables a dissociation of perceptual effects from response criteria or to combine perceptual judgments with additional variables that distinguish perceptual and response biases (Box 1). Another approach is to measure physiological correlates of perception such as microsaccades or pupil dilation that cannot be voluntarily controlled and are therefore unlikely to be affected by response biases. Finally, changes in neural correlates of early stages of perception such as activity in early sensory cortices or early components of electrical brain activity are unlikely to be impacted by cognitive judgment processes and therefore provide good evidence for cognitive penetrability. We focus on evidence from these and similar paradigms that can be unambiguously attributed to changes in the actual percept.

Box 1 How to reliably identify changes in perception

Behavioral studies that claim cognitive penetrability of perception need to demonstrate changes in the perceptual experience and rule out changes in the emotional or cognitive evaluation of that perceptual experience. Both a change in the participants' response criterion (the amount of sensory evidence internally required for a response; image panel a, solid and dashed line), which would not be classified as cognitive penetration of perception, as well as change in their internal stimulus representation (bottom panel, solid and dashed line), which would count as cognitive penetration of perception, can influence the probability with which participants report the presence of a stimulus (or of a difference between stimuli). Signal detection theory²⁴¹ enables experimenters to isolate participants' sensitivity to sensory information (their ability to detect sensory signals in the presence of sensory noise) from their



response criterion and thus reliably identify changes in perception.

Moreover, psychophysical studies using a forced choice design can measure changes in the just noticeable difference—the minimal change in the stimulus the individual can reliably perceive (see image, panel b dashed vs. solid horizontal line) — independent of shifts in perceptual and response biases (see image, panel b dashed vs. dotted dark line). For example, instead of requiring participants to report whether they perceived a difference between the roughness of two haptic stimuli, participants report which of the two stimuli felt rougher. The latter question measures the ability to detect differences between the stimuli by varying the roughness of one of them and without explicitly asking for differences. Changes in sensitivity or just noticeable differences due to cognitive information provide strong evidence for the cognitive penetrability of perception.

However, cognitive influences on perception will not necessarily result in a change in these sensitivity measures. For example, even if, due to a change in cognitive factors, all textures feel a little rougher, it might not be easier to distinguish between them, leaving the just noticeable difference unchanged. The shift in the percept towards rougher (panel c top, solid vs. dashed lines) can reliably be quantified using psychophysics, ideally in a forced choice discrimination or matching task rather than using ratings alone. Yet, a shift in participants' responses in itself does not always provide conclusive evidence. If in our haptic example one test stimulus is similar to sandpaper but the other one not, participants can always identify which one is which. If they now exhibit a tendency to categorize the sandpaper stimulus as rougher than the neutral one but do not do so for a stimulus reminiscent of carpet, it is impossible to know if their knowledge about sandpaper and carpets changed their actual percept, or just their tendency to report a stimulus as rougher than the neutral one. If participants indeed perceive the stimulus differently, the reaction time distribution (middle panel, solid vs. dashed line) should shift with the psychophysical curve. Thus, a shift in the percept should lead to a shift in the mode of the reaction time distribution that parallels the shift in the forced choice responses (see ²⁴² for an example). By contrast, a change in response bias should have hardly any effect on reaction times. To further support such a conclusion, experimenters can collect confidence ratings, indicating how confident participants are about the accuracy of their response. If a participant's percept changes, their confidence in the evaluation of this percept should change, too ²⁴³ (bottom panel, solid vs. dashed line).

Evidence across the senses

For the purpose of this Review, we define cognitive penetration as a change of perceptual experience through the influence of a higher cognitive content, such as a semantic memory content, abstract or conceptual knowledge, or a belief or intention (in line with ⁴). The change in perceptual experience cannot be caused by a change in external stimulus conditions (such as lighting or background noise), a change in a sensory organ (such as eye movements, sensory loss, or pathological conditions), or shifts of exogenous or spatial attention. With respect to the penetrated perceptual experience, we take the perspective of experimental psychology and restrict perceptual experience to experimental measures of objective task performance. We distinguish between veridical changes of perceptual experience and response bias of that perceptual experience.

We focus on senses with a dedicated sensory system in the brain (and as such exclude interoception, for example). Thus, we discuss perceptual experience in vision, audition, somatosensation, vestibular processing, and chemosensation. We do not discuss cross-modal interactions or multisensory integration in detail, because such mechanisms have been reviewed elsewhere ^{36,37}. In cases where sensory experiences are inherently

multisensory (for instance, flavor perception is a combination of taste and smell), we focus on the multisensory perceptual experience rather than integrative aspects.

Vision

In vision, evidence in favor of cognitive penetrability has been reviewed and discussed in depth by both philosophers and psychologists ^{1,3,5,6,8,9}. Many studies were not designed with the cognitive penetrability thesis in mind and therefore did not explicitly distinguish perceptual measures from response biases. However, many other studies do demonstrate changes in perceptual experience due to cognitive influences independent of response biases.

Studies measuring visual sensitivity (d')—which rules out shifts in response biases—present substantial evidence for cognitive factors influencing vision. For example, high-level cognitive image content cued by spoken words, verbal cues or naturalistic sounds increases visual sensitivity and image recognition of masked stimuli or stimuli suppressed from visual awareness, relative to uninformative or semantically incongruent stimuli ^{38–41}. Similarly, object recognition in two-tone, black and white images is difficult without prior knowledge (Fig. 2B). Previous exposure to the full grayscale image (Fig. 2e) increases visual sensitivity to edge detection in these images, even when the images are task-irrelevant, attention is controlled and visual stimulation remains identical ⁴² (see also ⁴³ for confirmatory results not measuring d' but with additional EEG evidence). Furthermore, in an ambiguous display in which moving balls can either bounce or cross, imagined sounds of colliding objects promote the visual perception of bouncing balls ⁴⁴. Thus, both early visual feature detection and object recognition in noisy and ambiguous visual situations are enhanced by cognitive information, while ruling out confounds of response biases.

Another way to circumvent the problem of response biases is to measure neural or physiological correlates of early vision that cannot be voluntarily controlled. Given that the vast majority of visual perceptual experiences, even when imaginary or unconscious, involve early visual cortex ^{28,45} and the eyes, cognitive influences on these respective correlates are very likely to affect perception, too. For example, the involuntary pupil response has been shown to be modulated by higher level cognition, even when controlling for general effects of attention and arousal ⁴⁶. For example, pictures containing a sun lead to smaller pupil size (in expectation of higher luminance) than pictures containing a moon, even if the actual luminance of the pictures is the same ^{47–49}. Similarly, listening to words that convey a sense of brightness or darkness (such as 'day' or 'night') ⁵⁰, imagining bright or dark objects ⁵¹, and maintaining bright or dark objects in visual working memory ⁵² modulates pupil size according to whether a bright or a dark visual stimulus is expected, even when actual visual input is minimal or absent. Even words with a positive meaning (such as 'victory') elicit pupil responses in expectation of brightness compared to words with negative meaning ⁵³. Together, these findings indicate that high-level cognitive concepts modulate the visual system at the very early level of the pupil.

Neural representations of visual stimuli, particularly in early visual cortex, are not under voluntary control and are therefore unlikely to be directly affected by response bias. Cognitive influences on these neural visual representations are often measured as changes in functional magnetic resonance imaging (fMRI) activity patterns using multivariate pattern analysis ⁵⁴. For example, there is accumulating fMRI evidence that the cognitive demands of tasks directly impact neural visual representations of identical stimuli, independent of attention, and all along the visual hierarchy down to primary visual cortex V1 (Fig. 3) (see ⁵⁵ for a review). For

example, V1 and V2 activity patterns in response to the same animal image differ significantly depending on whether the task is to categorize the image as a dog or a mammal. Even mere anticipation of the task changes activity patterns in early visual cortex before the visual stimulus is shown⁵⁶. In other similar studies, task (such as discriminating color or discriminating tilt) modulates neural activity patterns for identical objects in early visual cortex, as well as along the ventral visual object-processing pathway⁵⁷. These results suggest that early vision gets tuned to the features of the environment that are particularly task-relevant, and that behavioral goals directly impact visual representations of identical objects. Many visual brain areas upstream from V1, and equally responsible for functional visual perception (such as high-level visual cortices⁵⁸ and category-selective regions for face⁵⁹, word⁶⁰, and object⁶¹ recognition) are influenced by task.

Apart from tasks, many cognitive activities modulate neural representations in early visual cortex via top-down feedback. These include active mental imagery⁶², visual expectations^{63,64}, memory retrieval⁶⁵, learned conceptual associations⁶⁶, working memory content^{67,68}, action execution and action preparation^{69,70}, haptic shape exploration⁷¹ and listening to complex natural sounds^{72,73}. These changes in neural representations in early visual cortex do not occur with any unspecified cognitive activity (and therefore cannot be attributed to attention) but rather are content-specific or stimulus-specific. Furthermore, many cognitive influences lead to a specific change in neural tuning⁶⁶ or a sharpening of the precision of visual representations^{64,70,72}. Many studies present strong effects of top-down neural processing in vision^{20,74,75}, in accordance with evidence for the recurrent stream architecture of the visual system^{21–24} demonstrating that visual perception always involves both bottom-up and top-down processing (Fig. 3).

These results render the possibility of an informationally encapsulated visual module highly implausible. Instead, accumulating behavioral and neural evidence supports the idea that many different types of cognitive activities have a deep and manifold impact on visual perception and visual brain processes. These impacts occur across all visual brain areas and at the level of the eye and support the close integration of the visual system with many high-level cognitive brain systems.

Audition

Unlike in vision, few studies in audition have directly addressed whether auditory perception exhibits cognitive penetrability. Instead, evidence comes from a range of studies exploring specific questions, such as the influences on sound perception from expectations based on likely sound structure, explicit cuing, short-term statistics, and long-term learning. Experiments not specifically designed to address cognitive penetrability of audition nonetheless offer behavioral and neural evidence relevant to the question.

Top-down expectations strongly influence auditory perception across different experimental paradigms. In the phonemic restoration paradigm, listeners hear speech interrupted by temporal gaps that are filled in by noise. Instead of hearing discontinuous speech, listeners subjectively perceive complete words, and do not realize that their knowledge and expectations supplied the missing information (Fig. 2D). Moreover, listeners show improvements in objective measures of speech perception. Indeed, filling the gaps in with noise makes listeners perceive the interrupted speech as if the missing phonemes were actually present⁷⁶ (see⁷⁷ for a review). Simpler non-speech stimuli display a similar ‘continuity

illusion': Listeners perceive a sound that is interrupted by silence as continuous if noise is presented during the gap ^{78,79}. Experiments using similarity ratings ⁸⁰ and measures of perceptual sensitivity ^{81,82} demonstrate that these phenomena represent true changes in the perception of interrupted sounds, not simply a bias in how sounds are labeled. In both phonemic restoration and the continuity illusion, high-level knowledge of and expectations about sound structure override pure sensation to dominate perception. More generally, preceding speech inputs enable prediction of upcoming speech at the level of phonemic, lexical, and semantic structure ⁸³. Indeed, such top-down expectations even influence speech perception retroactively, changing perception of preceding ambiguous speech to be consistent with later inputs ^{84,85}.

Explicit priming also influences auditory perception. Naïve listeners might not even recognize that severely degraded speech (such as noise-vocoded speech or sine wave speech) is a speech signal. Priming with a preview (acoustic or visual) of the speech content before the degraded speech qualitatively changes perception so that the degraded sound is heard as speech⁸⁶⁻⁸⁸. Moreover, such priming of degraded speech, as well as priming from semantically related content, improves objective measures of speech intelligibility compared to when the same speech is presented without being primed ⁸⁶⁻⁸⁸, confirming a true perceptual change. Semantic priming by a related word, sound, or picture also impacts perception of non-speech, environmental sounds, speeding up identification reaction times, and reducing error rates compared to when there is no preceding primer ⁸⁹⁻⁹¹.

Auditory perception also varies with experience and learning across a range of time scales. Rapid learning is exhibited in listener adaptation to talker accent, which occurs as rapidly as over the course of a few words ⁹²⁻⁹⁶. Explicit cueing of talker identity enhances such effects, improving speech understanding compared to when the same accented speech is heard without cognitive knowledge of the talker identity, demonstrating a role for explicit knowledge on perception ⁹⁷. Long-term learning also strongly influences perception. For instance, listeners show a remarkable sensitivity for implicitly learning random patterns of tones or noise exemplars such that, when tested (even weeks) later, the previously heard examples are more easily detected than novel, similar patterns ⁹⁸⁻¹⁰². Together, these studies demonstrate that learning directly influences how sounds are perceived.

In addition to behavioral results, neural evidence supports the idea that cognitive processes interact directly with auditory sensory representations. During phonemic restoration, activity in the auditory regions that represent the acoustic properties of speech (including middle temporal gyrus and superior temporal sulcus¹⁰³ reflect the illusory percept, not the disrupted sensory inputs. These results provide direct physiological evidence that top-down expectations alter speech perception ¹⁰³⁻¹⁰⁵. Similarly, auditory cortex responds to continuity-illusion stimuli as if the input sound were truly continuous ^{81,106}. When processing degraded speech, priming by a preview of the original speech signal strengthens various neural markers of speech coding in auditory sensory areas ¹⁰⁷⁻¹⁰⁹. Similarly, priming from semantically related content strengthens the neural responses to subsequent degraded speech ⁸⁸ and semantic priming by a related word, sound, or picture changes the neural response to a subsequent sound ⁸⁹⁻⁹¹. In speech perception, predictions from preceding speech cause neural feedback onto auditory areas that encode incoming speech inputs, shaping how these representations code the subsequent speech and directly altering perception of the later speech ¹¹⁰⁻¹¹². Such cognitive influences on neural sensory coding also are reflected in learning paradigms. Specifically, the neural coding of sounds changes due to learning: the brain responds more robustly to learned, behaviorally relevant nonspeech sounds compared to similar but

behaviorally irrelevant sounds¹¹³ non-native language contrasts following training of those contrasts compared to before training¹¹⁴ and training of novel sound categories changes neural representations such that learned categorical distinctions can be decoded from neural responses in auditory cortex, while behaviorally irrelevant distinctions present in the training stimulus set cannot be decoded¹¹⁵. These studies provide support for the idea that memory processes feed back onto auditory sensory representations to directly influence auditory perception of sounds that listeners learn are relevant to their perceptual goals.

Attention modulates neural responses in the auditory system much as it does in vision, enhancing responses to an attended sound stream and suppressing responses to an ignored sound stream (for a review see¹¹⁶). Attention can be focused on a spatial location, or on non-spatial features such as timbre, pitch, or talker identity¹¹⁷, although spatial auditory attention more strongly engages prefrontal and parietal cognitive control regions often associated with visual attention than does non-spatial auditory attention^{118–122}. Modulatory effects of spatial attention are considered akin to effects changing the sensory organ (such as moving the eye) and not thought to be evidence of cognitive penetrability. Yet, non-spatial auditory attention modulates early auditory sensory responses such as the N1-P2 event-related potential complex in a manner similar to modulation by spatial auditory attention¹²³. This non-spatial attentional modulation of auditory responses therefore provides a robust example of cognitive influences on perception.

Other auditory paradigms also demonstrate changes in early sensory responses with changes in task demands. For instance, in a match-to-sample task, event-related potentials evoked by statistically identical stimuli differ depending on whether listeners are asked to recall location or pitch^{124–126}. Indeed, the kind of information a listener is holding in memory alters the amplitude of sensory-evoked auditory responses, providing another direct example of cognitive factors altering sensory neural coding¹²⁷.

Together, these examples suggest that cognitive effects on perception are widespread in the auditory system. Although information moves through an ordered stage of specialized processing regions, each has reciprocal connections with the previous stage. Rather than discrete, separable stages within a hierarchy, the auditory system is better described as a processing heterarchy¹²⁸: information at each stage of processing interacts with and influences information represented at other stages, with no clear simple line separating perceptual from cognitive processing.

Somatosensation

The somatosensory system underlies perception of touch, proprioception (the perception of body posture), and pain. Each of these modalities is processed along specific pathways (which in the case of touch and proprioception merge along the cortical processing hierarchy¹²⁹) and therefore we discuss them separately. Somatosensory perception is anything but an encapsulated process: vision tends to dominate tactile^{130,131} and proprioceptive¹³² perception, there are strong attentional influences on tactile perception¹³⁰, and tactile illusions suggest an influence of prior sensory experience^{30,133}. However, few published studies have tested for effects of higher-order cognitive processes on somatosensory perception. Moreover, several of the studies that test cognitive influences on somatosensory perception use measures that are susceptible to response biases, which prevents a final and general conclusion about the

penetrability of somatosensory perception. Instead, a differentiated pattern emerges across the different sub-modalities.

Tactile spatial perception requires a representation of the shape of the body. Changes in the representation of body shape can be elicited through conflicting visual information, action feedback manipulations ¹³⁴, tool use ¹³⁵, or through hypnosis ¹³⁶. Manipulations of the perceived size of the body impact the perceived size of objects touching the manipulated part of the body. Perceptually-enlarged body parts are associated with perceptual biases towards larger tactile distances ¹³⁷ as well as better spatial resolution ¹³⁸ and changes in tactile masking consistent with reduced tactile receptive field sizes ¹³⁹, which cannot be explained by mere response biases. Thus, a large body of research suggests that tactile spatial perception is cognitively penetrable. Yet, the cognitive influence is indirect in that changes in the perception of an object are due to changes in the representation of the body part touching the object rather than changes in the representation of the object itself.

Pleasant or affective touch, that is, tactile stimulation elicited by stroking with low velocity and soft pressure ¹⁴⁰, is subserved by a different type of receptors and processed along a separate neuronal pathway than mechanical touch ¹⁴⁰. The cognitive penetrability of pleasant touch has high face validity: A caressing touch feels different depending on the identity and presumed intentions of the person doing the touching. However, changes in the pleasantness ratings and bodily reactions to pleasant touch across contexts ¹⁴¹ might exclusively reflect emotional evaluation of the touch and thus not reflect an effect on perception. In support of cognitive effects on perception itself, the emotional expression of the person stroking the participant affects early components of the characteristic changes in electrocortical activity associated with the tactile stimulus ¹⁴². Similarly, the presumed (not actual) gender of the toucher modulates activity in primary somatosensory cortex ¹⁴³. However, other studies do not implicate primary somatosensory cortices in the encoding of pleasant tactile sensations ¹⁴⁴ which has raised the question why cognitive influences lead to changes in activity in this area. In sum, few studies unambiguously show cognitive penetration of affective touch.

The cognitive penetrability of proprioception has predominantly been investigated behaviorally, in the context of the rubber hand illusion ¹⁴⁵. In this illusion, visual-tactile stimulation, such as synchronous stroking of a visible rubber hand and the participant's real, hidden hand, leads to feelings of ownership of the rubber hand (embodiment) and mis-localization of the real hand towards the rubber hand (proprioceptive drift). These body-image-related and proprioceptive effects of the rubber hand illusion are dissociable. Manipulations such as rotating the rubber hand into an impossible position or stroking the real and rubber hands asynchronously influence the embodiment of the rubber hand but do not eliminate the proprioceptive drift ^{146,147}. Proprioception is drawn towards the location of the rubber hand even when contextual information should prevent this drift. Hence, cognitive processes cannot prevent the integration of proprioceptive and visual information, suggesting that proprioception is cognitively impenetrable ¹⁴⁸.

Haptic perception, also known as active touch, requires the integration of tactile and proprioceptive information over time. Several studies have shown cognitive influences on the haptic perception of textures. However, these results were acquired with questionnaires ¹⁴⁹ and psychophysical methods ¹⁵⁰ and therefore might index changes in response biases rather than perception. Similarly, knowledge about an object changes haptic perception of that object

¹⁵¹ and the associated network of brain activity ¹⁵², yet, these results could also be explained by changes in the cognitive evaluation of the perceptual information. Thus, haptic perception might well be cognitively penetrable, but additional measures are needed for a definitive conclusion.

Placebo effects are among the most impressive demonstrations of cognitive penetrability of sensory perception – and have enormous practical relevance. Placebo effects refer to any improvements to the well-being of patients based on exposure to cues that are part of a typical medical intervention, such as receiving inert sugar pills or visiting a doctor's office. Placebo effects typically do not impact the medical condition (for instance do not lead to shrinkage of a tumor) rather they alter the subjective symptoms associated with the medical condition ¹⁵³. Analgetic (pain-reducing) placebo effects established using subjective measures might reflect response biases or changes in the emotional evaluation of pain and are therefore not considered here. However, analgetic placebo effects are also evident in physiological indicators of sensory processing. For example, neuroimaging studies that combine moderately painful stimuli (such as heat) with a placebo show that placebo treatments impact neural activity in several areas involved in pain perception such as somatosensory cortices, the insula ¹⁵⁴, and thalamic nuclei ¹⁵⁵. These areas are involved in early sensory processing of pain, thus, modulations in these areas provide evidence for the cognitive penetrability of pain perception. These placebo effects vary with the strength of the analgetic effect ¹⁵⁶ and the experimental manipulation of the study ¹⁵⁶. The top-down pathways involved in these sensory modulations are still under debate but there is emerging consensus that placebo effects go beyond conditioning and are rather based on learned cognitive associations ¹⁵⁷.

In sum, there is good evidence for the cognitive penetrability of pain perception as well as some tactile perceptual processes and some evidence against the cognitive penetrability of proprioception. Percepts that rely on the integration of sensory information and prior knowledge seem most likely to be penetrable (except for proprioception). The strongest evidence for cognitive penetrability of somatosensation comes from studies of analgetic placebo effects. It might be that the complex mechanisms underlying pain perception are more penetrable than, for instance, simple proprioception. Yet, the stark contrast between the small number of studies testing higher-level cognitive influences on other types of somatosensation and the large number of studies testing these influences in pain perception stands out. Ultimately, this disproportionate evidence raises the possibility that the weak evidence for cognitive penetrability in some modalities is simply a consequence of fewer definitive studies addressing the question.

Vestibular perception

Vestibular processing involves interpreting information about one's body motion and orientation in its surroundings and is essential for spatial orientation, balance control, and motor coordination. The vestibular system originates from a sophisticated set of sensory transducer organs within the inner ear. Three perpendicular semicircular canals (anterior, posterior, and horizontal) detect rotational acceleration of the head along the yaw, roll, and pitch axes and two otolith organs (the utricle and saccule) jointly sense translational acceleration, including gravity. Vestibular signals are relevant to several interactions between the organism and its environment. Specifically, dynamic vestibular inputs from the semicircular canals influence visuo-vestibular interactions for self-motion¹⁵⁸, whereas static gravitational inputs from the otolith organs play a role in path integration and navigation¹⁵⁹.

Unique among the sensory modalities, vestibular inputs lack a clearly defined phenomenological experience. The object represented by vestibular signaling is the body orientation in the three-dimensional space. Consequently, unlike the perceptual experiences induced by specific stimulus objects – such as seeing a red apple, hearing a familiar voice, or feeling a mosquito on the skin – vestibular signals do not generate distinct, noticeable, salient perceptual contents. Instead, vestibular signals create a backdrop for all of one's activities. Additionally, vestibular inputs do not project to a primary unimodal cortex, analogous to primary visual cortex V1, primary auditory cortex A1, or primary somatosensory cortex S1. Instead, multimodal convergence between vestibular, visual, somatosensory and proprioceptive cues has been observed in nearly all vestibular relays, including the brainstem vestibular nuclei, thalamus, and several areas in the cerebral cortex ¹⁶⁰. Electrophysiological studies in non-human primates have identified a widespread vestibular network whose core area is the so called Parieto-Insular-Vestibular Cortex (PIVC) ¹⁶¹. The human homologue of the PIVC is a distributed set of regions including the posterior and anterior insula, temporo-parietal junction, superior temporal gyrus, inferior parietal lobule, and somatosensory cortices (see ¹⁶² for a review). With this broad neural distribution, vestibular signals play a role in a range of cognitive functions from sensorimotor control to the highest levels of consciousness ^{163–167}.

Our focus is on whether cognition penetrates pure vestibular processing: behaviour involving the activation of vestibular peripheral organs, whether through actual movement in the environment or via artificial stimulation. We therefore concentrate on vestibular processing related to balance. Balance is the coordination between sensory input, neural processing, and motor output that enables an organism to maintain postural stability and equilibrium. This coordination involves integrating information from various sensory systems, including the vestibular system, proprioception, and vision, to continuously adjust muscle activity and body position in response to environmental changes. Then focusing on vestibular processing for balance, there is no clear evidence supporting cognitive penetrability, meaning that the brain's mechanisms responsible for processing vestibular information operate independently of higher cognitive functions like belief or expectations. This suggests that the vestibular system processes sensory input in a way that is not influenced by cognitive processing.

Although cognitive factors impact the visual channel of balance control¹⁶⁸, the vestibular channel seems to be automatic and immune to cognitive knowledge. When individuals are aware that an upcoming visual disturbance is likely caused by an external source, such as a change in the visual environment, rather than by vestibular self-motion, the whole-body sway balance reflex, an automatic response that stabilizes posture by adjusting muscle activity to counterbalance disturbances or changes in position, thereby preventing falls, is suppressed ¹⁶⁸. However, whole-body sway balance responses to purely vestibular-induced disturbances remain unchanged even when individuals are aware that a vestibular disturbance is likely to occur. Studies have explored the whole-body sway reflex response to a pure vestibular perturbation induced by artificial Galvanic Vestibular Stimulation, a non-invasive technique that stimulates the vestibular nerve via electrodes placed on the mastoids¹⁶⁹. Often a bipolar-binaural configuration is employed, where anodal currents reduce vestibular nerve firing rates and cathodal currents enhance them¹⁷⁰. Galvanic Vestibular Stimulation elicits an illusory self-motion sensation that prompts postural adjustments when standing ^{171,172}. Importantly, the whole-body sway reflex response to this pure vestibular perturbation seems unaffected by whether the vestibular stimulus is self-initiated, predictable, or unpredictable. That is, the expectation of a vestibular disturbance, whether through voluntary action or prior knowledge of an event and its timing, does not influence balance responses ¹⁷³.

The impact of other forms of cognitive modulation, such as changes in cognitive load, on balance control also seems to be inconsistent. Some studies indicate no difference in postural sway when individuals are required to perform a secondary task (dual-task paradigm)¹⁷⁴, whereas others report either a decrease in postural stability¹⁷⁵ or even a slight improvement^{176,177}. Taken together these findings suggest that, if present, the influence of cognitive load on balance control is rather modest.

In sum, current evidence suggests that vestibular processing is resistant to cognitive penetration. This impenetrability can be attributed to the fundamental nature of pure vestibular processing: the vestibular system provides a direct and unambiguous signal to the brain regarding the acceleration of the head in space. This inherent reliability of vestibular signaling might offer a foundation for the brain to adaptively respond to changes in the environment and maintain spatial orientation and balance. The ubiquity of vestibular signaling further reinforces its resilience against cognitive penetration. Given that the vestibular system continuously detects head motion and gravity, it generates a constant sensory flow from early fetal life until death and forms the basis for survival and efficient navigation¹⁶⁶. As such, the brain might prioritize the reliability of vestibular signals over cognitive influences to ensure behavioral adaptation, particularly in situations in which rapid and precise adjustments are required to maintain balance and avoid potential threats. The robust and reliable nature of vestibular processing might make it less susceptible to cognitive influence compared to other sensory modalities.

Chemosensation

The senses of gustation, chemesthesis, and olfaction form the body's principal detection system for chemical compounds, jointly referred to as chemosensation. The three chemical senses are clearly anatomically separable from each other in their peripheral sensory organs and produce distinct perceptual experiences in the form of taste, chemical irritation, and smell, respectively. These will be reviewed separately below, given that fundamental differences in neuroanatomy and guiding perceptual processing principles for the chemical senses likely impact their cognitive penetrability. These three contributing senses are very closely perceptually integrated when they co-occur in the oral cavity in the context of food consumption. In this context, source allocation to the specific sense is very restricted and an integrated percept emerges, typically referred to as a shared 'flavor sense' arising from the mouth^{178,179}. Cognitive penetrability of flavor perception as an integrated form of chemosensory perception will therefore be considered separately from penetrability of the individual senses.

The taste percept arises when water-soluble compounds make contact with gustatory receptors on the tongue, soft palate and pharynx¹⁸⁰, yielding five known separable perceptual qualities that are each linked to a specific evolutionary benefit or threat (for instance, sweetness indicating likely presence of carbohydrates, bitterness indicating likely toxicity) and are therefore thought to elicit innate approach and avoidance behavior (see¹⁸¹ for a review). There is strong evidence that these innate responses can be regulated by associative learning, in which an initially aversive taste becomes pleasant through association with an object with pleasant features^{182–184}.

Gustatory receptor stimulation by itself provides insufficient dimensionality for object recognition. For example, when a person experiences nasal congestion that blocks olfactory input, many fruits produce a diffuse sense of sweetness on the tongue, making it impossible to tell apart different fruits (such as a cherry and a blueberry) based on this information alone. Object attribution arises from associations with other sensory input, such as the color of the

food item, its texture, and most notably the volatile chemicals it releases, which produce an aroma of cherry or blueberry detected in the nose during consumption^{185,186}. These crossmodal inputs do not induce changes in the features of taste quality per se, but in its intensity and hedonic evaluation (pleasantness or unpleasantness). For instance, bitter taste is typically unpleasant, but not in the context of the aroma of freshly brewed coffee.

Multisensory effects on hedonic evaluation of gustation are object-specific^{187–189}, indicating that they are the result of associative learning and as such, cognitively mediated. Learned associations with specific colors that typically represent a particular object (for instance, red associated with cherry flavor) can result in tastes being perceived as, for example, more intensely sweet or sour, whereas the perceptual quality (sweetness or sourness) remains unchanged. Odors that typically co-occur with particular tastes can increase the perceptual intensity of a gustatory stimulus, a phenomenon known as odor-induced taste enhancement¹⁹⁰. Thus, high-level knowledge of and expectations about taste do not override sensation to produce a different percept entirely (as it can in senses such as audition) but can change its intensity or hedonic tone.

Few studies have explicitly attempted to identify the location in the processing hierarchy at which these influences arise. The limited existing neuroimaging evidence is in line with impenetrable early sensory representations of taste, with changes in intensity and valence attributions due to cognitive associations modulating taste-related activation in orbitofrontal cortex^{191–193}, and pattern coding in the primary gustatory cortex responding strictly to taste qualities along the five basic tastes^{194–196}. Further studies are needed to increase understanding of the neural processing hierarchy regulating taste associative learning.

Chemesthesis (the sense of chemical irritation in the skin and mucous membranes) is, like the sense of taste characterized by low dimensionality: evoked sensations are grouped into those that are experienced as hot and those experienced as cold, with variation referring to the extent of hotness or coldness observed. The sensations are evoked by chemical compounds activating temperature sensing transient receptor potential (TRP) channels of cutaneous nerve endings to induce the sensations of coldness (such as menthol, sensed by TRPM8 receptor activation) or heat (such as capsaicin, sensed by TRPV1 receptor activation) in the absence of actual changes in temperature. During food consumption, chemesthesis arises primarily from stimulation of trigeminal nerve endings in the mucous membranes of the mouth, nose, and eyes. The hedonic experience of these can be modified based on learning and experience¹⁹⁷ to be perceived as either pleasant or unpleasant. As such, these perceptions share some common characteristics with the more general experience of pain as reviewed above. The presence of trigeminal stimulation can increase sensitivity for olfactory and gustatory perception^{198–201}. There is some evidence that peripheral receptor-receptor interactions alter perceptual experience (such as simultaneous chemical stimulation of TRPM8 and TRPV1 inducing the thermal grill illusion in which a moderately warm and a cold stimulus combined produce a sensation of extreme heat²⁰²). Furthermore, learned crossmodal associations can modify the intensity of the perceptual experience^{203–205}. However, there is no evidence for cognitive penetrability of the sensory quality of the cooling or burning experience induced by chemesthesis. That is, there is no evidence to date indicating that spicy food can induce a cooling instead of burning perceptual quality through cognitive modulation.

In olfaction, sensory experience arises from airborne volatile chemicals that make contact with receptors in the olfactory epithelium at the roof of the nasal cavity, either by sniffing or by being pushed up the throat while food is chewed and swallowed. In contrast to the low dimensionality of gustation and chemesthesis, olfaction is characterized by extremely high

dimensionality: humans can functionally distinguish between an almost unlimited variety of odorous stimuli. Yet, labeling and recognition abilities are generally poor for individuals in Western societies, likely due to lack of training in associating learned labels with percepts²⁰⁶ and poor functional-anatomical integration with lexical knowledge²⁰⁷. Discontinuities in mapping of chemical structure to perceived odor are frequently observed²⁰⁸, in which odors are perceptually grouped together predominantly not by their chemical features, but instead by their frequent co-occurrence as part of the same object^{209,210}, which indicates that odor object perception is highly experience-dependent. For example, although citronellol and 3-octanol are both alcohols, citronellol is perceived as more similar in odor quality to the structurally dissimilar aldehyde nonanal due to their shared association with lemons, whereas the structurally similar 3-octanol is perceived as more vegetable-like²¹¹.

The olfactory perceptual experience is highly susceptible to cognitive interference^{212,213}. Multistable olfactory percepts based on knowledge or cognitive integration of various inputs can arise and switch spontaneously: the exact same stimulus can lead to a fundamentally different perceptual experience based on the associated label. For example participants have been shown to experience a combination of butyric and iso-valeric acid as cheese-like when labelled as “parmesan cheese” but to smell like vomit when labeled as “vomit”^{214,215} (Fig. 2E). Moreover, odor perception changes when odors are presented with particular colors^{216,217}, sounds²¹⁸ or under different metabolic states^{185,219}. Evidence increasingly points toward a Bayesian predictive coding framework underlying these findings^{220–222}, but the plasticity and maturation of these predictions over the life course, as well as their functional-anatomical implementation in the olfactory cortical network remain the subject of investigations (see²²³ for a review).

Human neuroimaging experiments and rodent studies demonstrate that learned object associations and contextual influences are encoded at the level of the primary olfactory cortex^{220,224–227}. Evidence for identity-dependent changes in gamma-band activity even indicates that perceived odor object identity might influence perceptual coding as early as the olfactory bulb^{228,229}. Unlike for taste and chemesthesis, high-level knowledge of and expectations about smell can override sensation to produce the percept of a different object representation. As such, behavioral and neuroimaging evidence converge towards a strong argument in favor of cognitive penetrability of the sense of olfaction.

Finally, perceptual experiences related to the chemical senses are tightly conceptually coupled during food consumption and typically perceptually merged into a shared representation of a quasi-synesthetic ‘flavor quality’. Although the merging of gustation, chemesthesis and olfaction into flavor is experience-dependent and therefore mediated by learning, it is highly robust to knowledge. For instance, perceivers are typically unable to experience aroma compounds of foods as arising from the nose, and commonly and persistently attribute reduced flavor perception from blockage of olfactory pathways as ‘taste loss’²³⁰. Furthermore, crossmodal enhancement effects such as a stronger percept of cherry flavor in a red beverage persist even when subjects are explicitly told that there is no relationship between the visually elicited object association and the flavor of the beverage, indicating that these associations can arise outside of voluntary control²³¹.

In summary, the chemical senses are characterized by diversity in peripheral and central processing mechanisms and there are differences in the extent of available research relevant to cognitive penetrability. The evidence base is strongest for olfaction, where ample evidence exists in favor of cognitive penetrability from behavioral and neuroimaging studies. The evidence base for gustation and chemesthesis is weaker and would benefit from the

development of new paradigms specifically suited to address the question of cognitive penetrability in these senses. Meanwhile, although low-level crossmodal effects have been documented, the available behavioral and neuroimaging evidence demonstrates only quantitative changes of gustatory sensations from cognitive influences, not qualitative changes, which might result from the lack of object processing capabilities of the gustatory sense. The evidence base for chemesthesis is even more limited and provides some weak evidence for cognitive penetrability that also takes the form of quantitative changes in experience. Relative impenetrability of gustation and chemesthesis might provide an evolutionary benefit, given the direct link of these sensations to ingestion of nutrients or toxins. This connection might also explain their pervasive and impenetrable effect on olfaction in the context of flavor binding, where odor experience is substantially shaped by the presence of these modalities.

Synthesis of evidence across the senses

In some senses, the evidence speaks quite clearly for cognitive penetrability, in other senses it speaks for cognitive impenetrability, and in some cases the evidence is mixed or simply incomplete. Evidence strongly supports cognitive penetrability of perception in vision, audition, olfaction as well as in pain and tactile perception. Conversely, evidence for cognitive impenetrability exists for proprioception and vestibular processing (apart from modest cognitive load influences on balance control and its visual aspects). Some evidence exists for cognitive influences on haptic perception and influences of the hedonic evaluation on affective touch, taste and chemesthesis, but it is difficult to disentangle whether these are true cognitive or more evaluative or emotional influences.

A note of caution is needed when comparing the evidence regarding cognitive penetrability across the senses. The current state of evidence depends directly on the type and amount of research that has been done in the respective fields. For example, vision and audition are traditionally more heavily researched than chemosensation, proprioception, and vestibular processing, and accordingly, much more evidence for cognitive penetrability exists in those former modalities. Research on pain perception and placebo effects is of high clinical and practical relevance and is accordingly well funded. Thus, a lot of evidence for cognitive penetrability has accumulated in this field. A lack of evidence for cognitive penetrability in vestibular processing, proprioception, and chemesthesis might therefore partly reflect the low volume of research in these senses. In a complex topic such as cognitive penetrability, the quantity of research matters in weighing the evidence.

With this caveat in mind, we discuss possible reasons for the observed differences across the senses and based on the type of influence.

Differences across senses

The answer to whether perception is cognitively penetrable depends heavily on which perceptual experience is being considered (Fig. 4). There are likely evolutionary reasons for these differences. Susceptibility of vision, audition, olfaction and parts of somatosensory perception to cognitive influences might be highly adaptive. Sensory information from these channels is complex, manifold, and potentially noisy and ambiguous. In such conditions, the organism might need to integrate prior experience, contextual information, and memory content to create a percept that provides the best possible representation of the outside world.

For example, the olfactory system can theoretically discriminate a much larger number of odors than could possibly be functionally relevant and the brain will classify these sensory experiences into “smell objects” based on associations with a shared source ^{208,232,233}. Similarly, in natural viewing and hearing conditions (that is, not under the controlled conditions of a laboratory), visual and auditory input is complex and often ambiguous (due to factors such as occlusion and masking) and needs to be ‘clarified’ by contextual information and previous expectations ^{75,234}. In touch, sensory processing is facilitated by temporal expectations ^{235,236}. Taking prior knowledge and context into account reduces the complexity and processing load of sensory information and makes this information predictable for the brain. Predictions are a key ingredient for fast, accurate and resource efficient processing to create a percept out of an overwhelming amount of sensory information ^{234,237}.

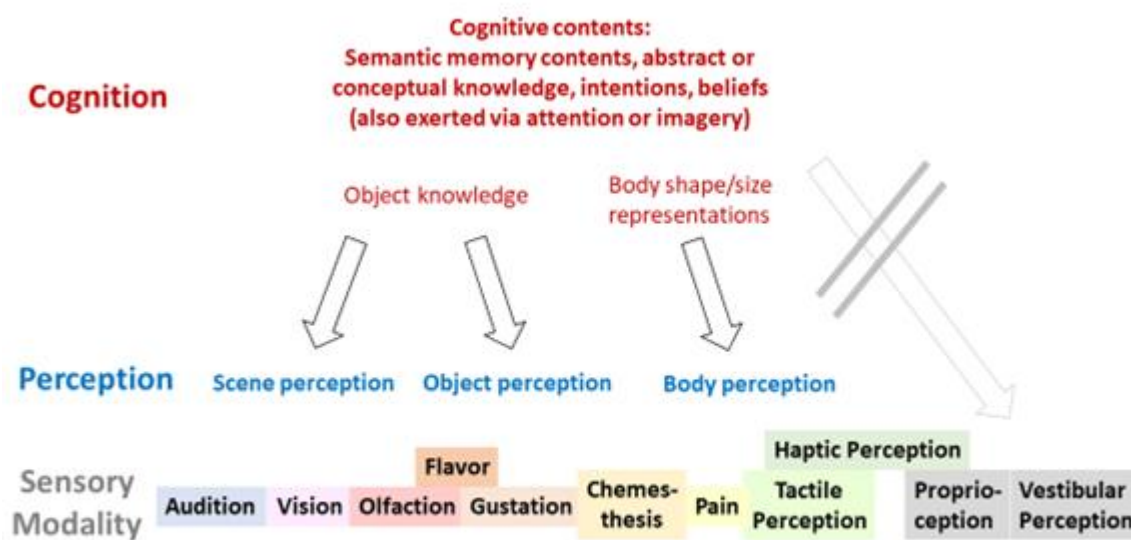


Figure 4. Influences of cognition on perception across the senses. Here, cognition is defined as a higher cognitive content, such as a semantic memory content, abstract or conceptual knowledge, a belief or intention, that can also be exerted via endogenous attention or mental imagery that carries cognitive information. Cognition can influence object and scene perception in audition, vision, pain and haptic perception (arising from a combination of tactile perception and proprioception), olfaction and gustation (with flavor arising from both smell and taste). Cognition also influences tactile perception via changes in body representations. By contrast, proprioception and vestibular processing (gray) are largely unaffected by cognition.

The fact that the vestibular system and proprioception seem to be mostly impenetrable by cognition might be related to their fundamental importance for conveying information not about the environment as in most other senses but about the position of the head and the body in space, which is crucial for the ability to successfully adapt to the external environment. Penetrability to cognitive influences might be maladaptive in these senses because the grounding of one’s body in space needs to remain stable and should not depend very much on context. Instead of a direct influence, the influence of vision on the vestibular system (such as for balance control) and on proprioception might provide an indirect way by which cognition can influence these bodily senses. For example, visual and vestibular signals are constantly

integrated to calibrate one's head position in space with respect to the eyes ²³⁸ and seeing a rubber hand is sufficient to induce proprioceptive drift ¹⁴⁷. These changes reflect a multisensory rather than cognitive influence, with the visual channel of vestibular and proprioceptive sensing being cognitively penetrable [the “whereas” didn't fit here - we do not want to express an opposition here].

The relative lack of penetrability of chemesthesis and gustation might be due to their lack of dimensionality, which makes these sensory qualities very distinguishable and therefore less prone to contextual adjustment (apart from their hedonic evaluation). However, evidence regarding cognitive penetrability of chemesthesis and gustation, especially neuroimaging evidence, remains incomplete. Lack of dimensionality fails to explain, however, why pain, a fundamental physiological response to physical body damage of low dimensionality, is so clearly cognitively penetrable. A possible explanation could be that cognitive penetration of pain might be a survival mechanism that enables at least temporary suppression of the pain response to ensure fundamental survival such as reaching a safe space or getting enough food despite injury or illness.

Cognitive penetrability of somatosensation seems to depend on the extent to which information from another sense and prior knowledge is integrated. In haptic perception, in which tactile and proprioceptive signals are integrated, cognitive knowledge about the touched objects affects haptic perception. Similarly, cognitive knowledge about body shape influences spatial perception of touch. On the other hand, integration of vision and proprioception in the rubber hand illusion seems to be resistant to cognitive influences, potentially because proprioception, as the vestibular system, provides basic information about the body rather than the environment.

Types of influences

In addition to distinguishing types of perceptual experiences by sensory modality, it might be equally important to distinguish types of influences that penetrate perceptual experiences – whether they are cognitive, emotional, or multisensory and whether they are direct or indirect influences. Although some senses might not be penetrable by higher cognitive contents, by their nature they are sometimes heavily influenced by information from other sensory modalities²³⁹. For example, vestibular, proprioceptive, tactile, and gustatory perception are highly influenced by visual signals, and vision is often cognitively penetrable. Thus, cognitive factors might assert an indirect influence on some sensory modalities via multisensory interactions. A similar argument can be made about attention and imagery: although not every cognitive factor can influence perception directly, it might do so indirectly by shifting feature or object attention or via an intermediate process of mental imagery⁴, including across sensory modalities.

Another interesting idea that emerges when considering multiple sensory modalities is that hedonic evaluation (for example, pleasantness /unpleasantness) [I think this needs to be in to explain what we mean by hedonic evaluation] of sensory information is intricately connected to its perceptual experience, for example, in affective touch ¹⁴⁰ and olfactory perception ²⁴⁰. In these modalities, the hedonic evaluation of the perceptual experience is an essential part of ‘what it is like’ to have this experience. In these instances, the theoretical distinction between perceptual experience itself and judgment of the percept's hedonic quality is not reflected in neural sensory processing and the functional and anatomical organization of the brain.

Furthermore, one could conceptualize hedonic evaluation as a cognitive process that is ingrained in the perceptual experience in these modalities, which would speak strongly in favor of cognitive penetration. Once again, the debate of cognitive penetrability strongly hinges on what counts as cognition and cognitive factors^{1,5}. What counts as cognitive determines whether, for example, prior object knowledge that influences haptic perception, or the expectation of redness that changes the sweetness of a fruit are instances of cognitive penetrability. Likewise, the abstract knowledge about the intentions of a person stroking one's arm could be considered cognitive, emotional or a judgment, with differing implications for cognitive penetrability.

Although theoretical debates make clear distinctions between words like 'cognition', 'evaluation', 'emotion', and 'perception', these distinctions map poorly onto brain functioning. Given the evidence that the brain is heavily interconnected within itself, and constant, fast and recurrent processing happens between and across a huge variety of brain regions, it seems difficult (and potentially even maladaptive and inefficient) to draw strict boundaries between these different processes. It is more likely that many of these brain processes happen concurrently and in parallel. For instance, seeing the redness of a fruit might activate the concept of sweetness, thereby biasing gustatory perception towards higher sweetness.

From the reviewed neural evidence, it is clear that every sensory modality engages a wide network of brain areas that interact closely with each other to create a conscious perceptual experience. It is highly unlikely that none of these areas are influenced by brain areas and processing streams that carry some kind of cognitive information. For example, the vestibular system, which seems comparably unaffected by cognitive influence, is nonetheless heavily crossmodally interconnected and could indirectly be influenced by, for example, visual object knowledge. Thus, our final conclusion is that although the extent to which cognition influences perception differs across the different senses, the postulation of 'informationally encapsulated' perceptual modules fails to hold true for any sensory modality. Instead, the reviewed evidence supports the notion that cognitive penetration of perception does indeed exist, and in the majority of sensory modalities such as vision, audition, olfaction, pain, haptic and tactile perception.

Summary and future directions

In this Review, we considered different sensory modalities to extend the debate on the cognitive penetrability of perception. First, we showed that some senses are more and some less penetrable by cognition, and others seem at best indirectly penetrable through cross-modal influences from penetrable senses. Thus, the question of whether cognition penetrates perception needs to be differentiated by sensory modality. Second, there are many different types of influences on perception (including cross-modal, evaluative, direct, and indirect) each of which carries some cognitive information, albeit to differential extents. Thus, the question of whether cognition penetrates perception depends very much on what is regarded as cognition. This distinction is a theoretical one rather than one that reflects how the brain operates, as supported by the reviewed neural evidence. 'Informationally encapsulated' perceptual modules are a rather implausible model for thinking about how perception unfolds. Instead, we conclude that the majority of perceptual experience is a result of rich interactions between cognitive, sensory, and multisensory processes.

In future research, we recommend that experimentalists in all sensory modalities address the question of cognitive penetrability of perception more directly, studying influences from clearly high-level cognitive states and avoiding confounding factors when measuring perception. We recommend carefully choosing experimental designs and measures that enable the researcher to distinguish perceptual experience from response bias (for example, by combining measures of d' , thresholds, reaction times and confidence ratings; Box 1). Furthermore, as mentioned above, the reviewed evidence might itself be biased by the number of studies that addressed the question of cognitive penetrability in each sensory modality. Thus, for a more complete picture of cognitive penetrability of perception, we recommend increasing the research effort, particularly in touch, haptic perception, proprioception, vestibular processing, gustation and chemesthesis. Illuminating how cognition can influence those senses could potentially be of clinical relevance, for example, in balance control, body perception and loss of flavor perception. For example, a better understanding of cognitive penetrability could help to determine whether cognition could influence balance training in patients with vestibular disorders, body image in patients with eating disorders or partial rehabilitation of flavor loss.

We also recommend that theorists draw careful distinctions among potential penetrating factors—especially with respect to different aspects of cognition, evaluation and emotion—and clearly define any further penetrating factors. Also, we strongly recommend incorporation of neuroscientific evidence into models of how the brain plausibly creates one's perception of the world. Overall, the reviewed evidence suggests that cognitive and perceptual brain processes are heavily intertwined, and that the brain provides a functional representation of the world that allows survival and is nevertheless not entirely determinable by our subjective thoughts. However, the exact intricacies of the interaction between cognition and perception do still require further careful investigation.

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Highlighted References:

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